12

The micro-environment of basidiomycete mycelia in temperate deciduous woodlands

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Introduction: resource relationships

Throughout this volume emphasis is placed on the mycelium as the basic unit of the fungus by which it obtains its nutrition and achieves vegetative spread. As such it is at this level that the most significant interactions between fungi and the biotic and abiotic environment occur. To consider all such interactions in the very many environments in which fungal mycelia are found would be an enormous undertaking. Thus, the approach adopted here will be to consider a particular case, that of basidiomycete mycelia in temperate deciduous woodlands.

The fruit bodies of Basidiomycotina in woodlands readily attract attention and it has long been known that these organisms are often the major agents of wood decomposition in both natural and man-made environments (Cartwright & Findlay, 1958; Swift, 1977; Rayner & Todd, 1979), although their importance has sometimes been obscured (Boddy & Rayner, 1983*c*; Cooke & Rayner, 1984). More recently their major role in the decomposition of non-woody litter has been emphasised (Frankland, 1982; Hering, 1982; Hintikka, 1982; Swift, 1982; Cooke & Rayner, 1984). Further, they interact with higher plants as parasites and as mutualistic symbionts forming mycorrhizal partnerships. However, despite their obvious importance to the functioning of the woodland system, their actual ecological roles and mycelial biology have received relatively little attention.

In woodlands a large proportion of organic matter, available to decomposers, derives from trees with 20–30% of the above ground input being woody, e.g. branches, trunks, twigs and the remainder leaves, flowers and fruits (Bray & Gorham, 1964; Boddy & Swift, 1983). The below-ground input is less easy to quantify but consists of non-

woody tissues, e.g. root hairs, sloughed cells, minor roots, along with large woody roots. Higher plants and bryophytes in ground vegetation also contribute to organic matter input as do animal remains and faeces. Although the input of woody material is much less than that of leaves, its more durable nature usually leads to considerable accumulation on the forest floor (Ovington, 1962; Swift, Boddy & Healey, 1984).

Thus the resources for growth of heterotrophs in this environment are considerable, ranging from bulky to finely divided, living to non-living, and are exploited by all of the three main nutritional modes of fungi, i.e. saprotrophy, necrotrophy and biotrophy. Relationships between basidiomycete mycelia and these resources can be considered to be of two types: those which are restricted to individual component units of the litter, e.g. individual leaves, twigs, flowers, branches, and those which are not restricted by physical bounds and can ramify throughout entire litter systems (Cooke & Rayner, 1984). Examples of the former include species of *Marasmius* and *Mycena* which are restricted respectively to the petiole and lamina of fallen leaves (Fig. 1*c*,*d*), species of *Mycena* on beech cupules (Fig. 1*b*); wood-rotting fungi such as *Coriolus versicolor* and *Stereum hirsutum* which are restricted to the wood unit which they occupy. Cord-forming fungi (Thompson: Chapter 9) and litter-decomposing organisms such as *Clitocybe nebularis* and *Marasmius wynnei* (Fig. 1*a*) are non-component restricted and ramify through the litter for considerable distances.

Many species and even genera appear to be specifically associated with a particular type of resource/substratum. For instance mycorrhizal fungi are predominantly members of the genera *Amanita, Boletus, Lactarius, Russula* and *Tricholoma*; members of the Aphyllophorales are mainly wood-rotters; and those which decompose leaf and non-woody litter are found mainly in the genera *Collybia, Clitocybe, Marasmius* and *Mycena.* Further some fungi are specific to certain plant taxa, e.g. *Piptoporus betulinus* on *Betula* trunks and branches, *Amanita muscaria* in mycorrhizal association with *Betula*, *Pinus* and perhaps *Carpinus*, and *Russula mairei* with *Fagus.*

On the other hand some Basidiomycotina utilise several different resource types: *Hypholoma fasciculare* and *Tricholomopsis platyphylla* are mycelial-cord-forming fungi which decompose large woody substrata, twigs and leaf litter (Thompson: Chapter 9); some mycorrhizal formers such as *Laccaria laccata* (Hering, 1982), *Boletus* spp. and *Tricholoma* spp. (Cooke & Rayner, 1984) are also able to decompose leaf litter.

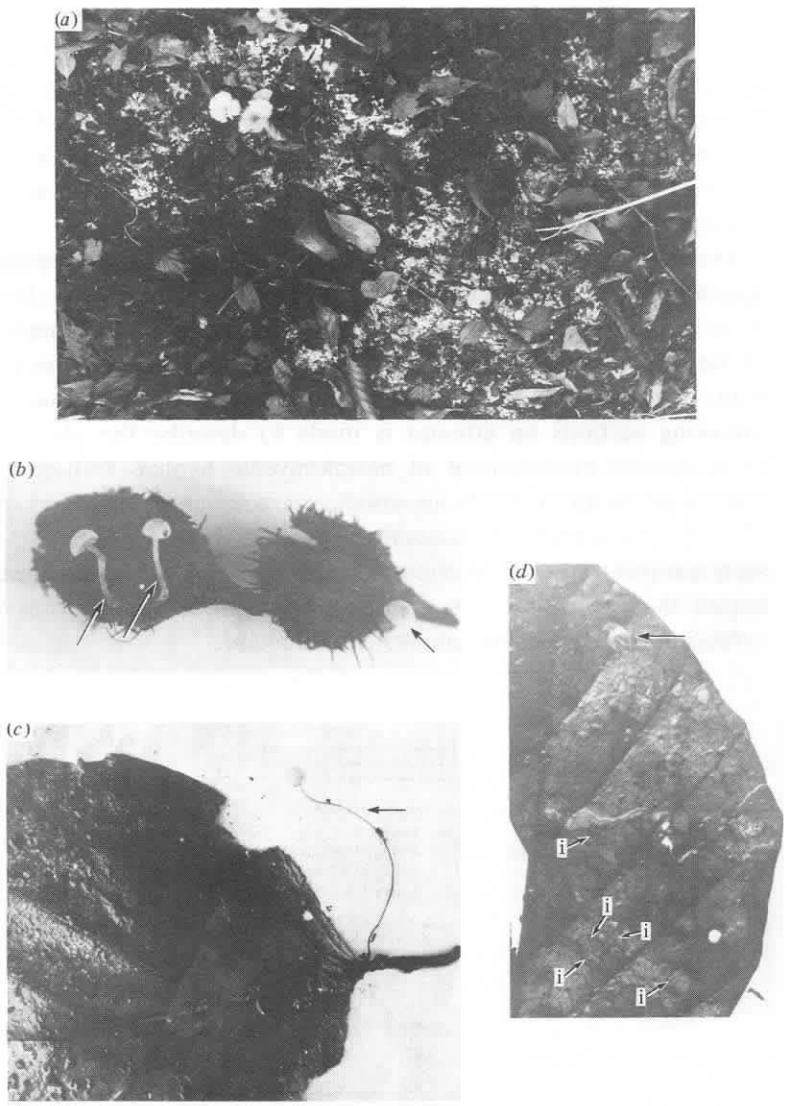


Fig. 1. (a) Non-component-restricted mycelium of *Marasmius wynnei* in deciduous litter. (b–d) Component-restricted basidiomycetes from beech (b) *Mycena* species (arrowed) fruiting on cupules. (c) *Marasmius* species (arrowed) developing from a leaf petiole. (d) *Mycena* species (arrowed) on a leaf lamina. Notice the probable interaction zone lines (i) between bleached regions. (From Cooke & Rayner, 1984.)

Evidently, then, each resource type in a deciduous woodland is characterised by rather specific associations of fungi. This is in accord with the concept of the unit community discussed by Swift (1976) and, such assemblages characteristic of a particular resource type are the nearest fungal approach to the concept of the plant association (Cook & Rayner, 1984). This raises questions of the origin of such specificity; the answer must lie in the interactions of Basidiomycotina with the abiotic and biotic components of the micro-environment associated with each resource type.

The main factors influencing basidiomycete mycelia are represented diagrammatically in modular form in Fig. 2. From this it is clear that there are numerous interactions between parameters: the components of the three modules interact with basidiomycete mycelia, with components of other modules, and with other components in a module. In the following sections an attempt is made to describe the physical and microclimatic environment of basidiomycete hyphae and mycelia in natural substrata in deciduous woodlands; to quantify the effect of such variables on fungi in the laboratory; and on the basis of this to relate such features to the distribution of basidiomycete mycelia in nature. It is hoped that principles will emerge from this discussion from which extension to other environments can be made.

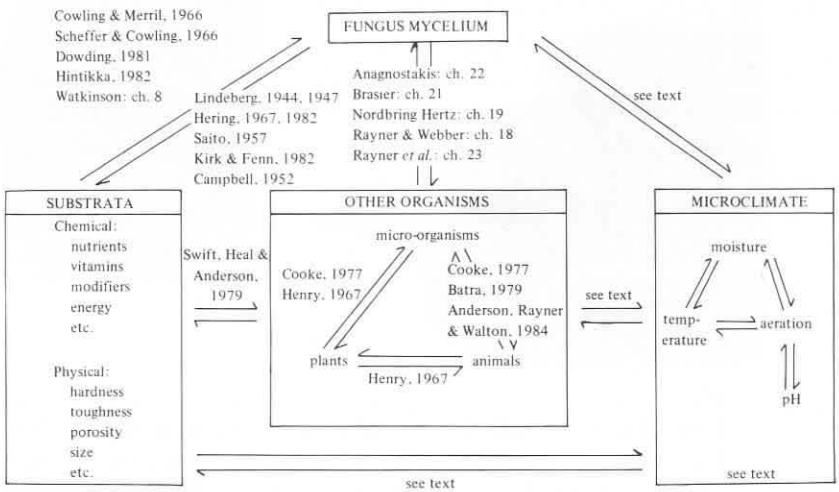


Fig. 2. Schematic representation of interactions between the fungus mycelium and the biotic and abiotic environments.

Physical and microclimatic environment

Substrata in which fungal mycelia are growing, be they soil, leaf litter, wood etc, may be regarded as matrices consisting of a solid phase comprised of variously sized organic/inorganic particles, and a system of voids. These voids occur both within organic material, e.g. vascular elements, cavities resulting from decomposition, and between the different inorganic and organic components (Fig. 3). They vary considerably in size from intermolecular spaces to cavities several millimetres or even centimetres wide. These voids are routes for entry of hyphae into the matrix, or a space which has to be crossed in order to reach another supply of organic nutrients, and are filled with a gaseous or liquid phase. Wherever hyphae are growing they will be affected by the physical and chemical conditions in the void.

Fungi interact with the environment at the hyphal level. However, the fungal hypha does not act entirely independently being only a small part of the fungal mycelium, which is a three-dimensional entity often occupying several cm^3 and sometimes even many m^3 (e.g. Thompson & Rayner, 1982, 1983; Boddy & Rayner, 1983*a,b*; Watkinson: Chapter 8; Thompson: Chapter 9; Frankland: Chapter 11). Thus, the mycelium has the unusual property of being located in numerous places at any one time and therefore may be subject to many different environmental regimes simultaneously. In terms of survival, resource capture and spread, it is the influence of biotic and abiotic variables at the mycelial level, resulting from the combined effect of these variables at the hyphal level, which is of relevance to the fungus.

Elucidation of the influence of micro-environment on the mycelium is not easy but considerably less difficult than for individual hyphae. It requires characterisation of conditions in the field along with quantification of the effects of such conditions on the mycelium. The latter can be achieved in the field but very often recourse is made to the laboratory. Extreme caution must, however, be exercised when extrapolating from artificial media, as these are necessarily relatively homogeneous whereas in nature heterogeneity is often the rule.

Temperature

Woodland and substratum microclimate reflects the local climate; thus temperature accordingly changes cyclically each day and during the year (Figs. 4, 7). It is, however, modified by various environmental features and differs from local temperature as a result of differences in aspect, degree of exposure to insolation and the buffering

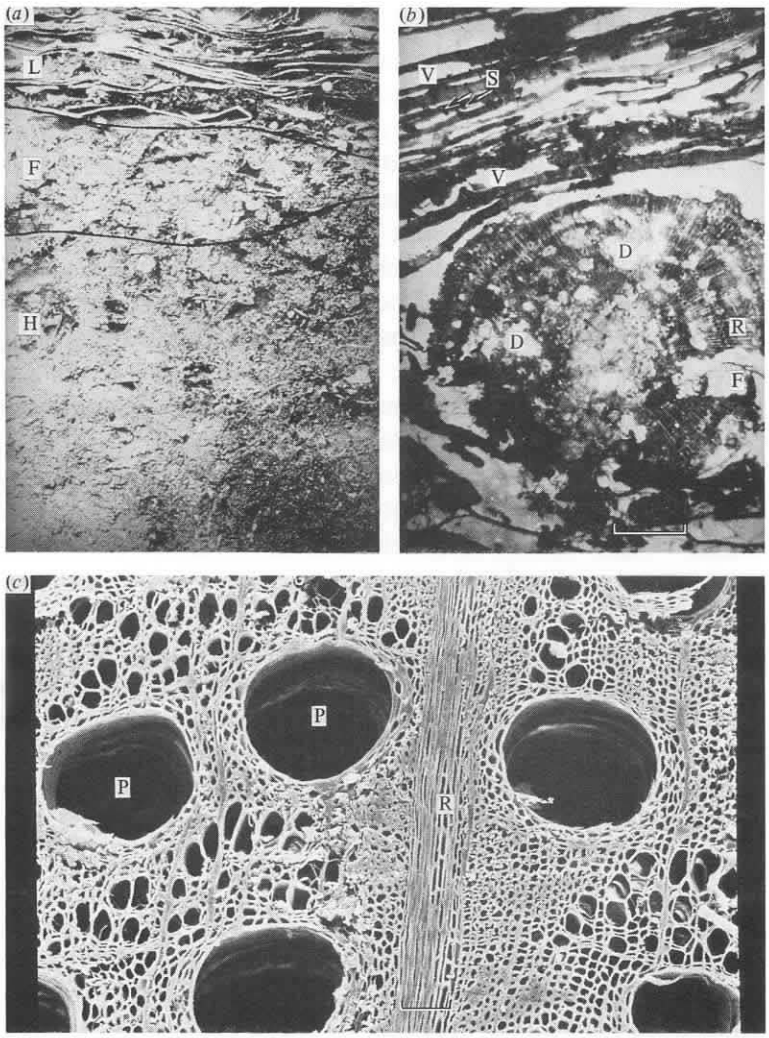


Fig. 3. Examples of microhabitats of fungal mycelia within organic substrata at different scales of resolution. (a) Detail of a gelatin-embedded vertical section through the top 5 cm of a well-developed organic soil in a *Castanea sativa* woodland showing the litter (L), fermentation (F) and humus (H) sub-horizons. (From Swift *et al.*, 1979.) (b) Detail of a section through the litter layer and a rotten twig in the same site as (a) illustrating voids between leaves (V), voids resulting from decomposition of substrates (D), and anatomical voids of the vessels and medullary rays (R). Fungal hyphae innervating twig from surrounding leaf litter (F); dark fungal stroma on leaves (S); scale bar, 1 cm (from Swift *et al.*, 1979.) (c) Scanning electron micrograph of oak sapwood showing different sized vessels (P) and medullary ray cells (R). Scale bar, 100 μm. (From M. Hale, unpublished.)

effect and different thermal capacities of the surrounding vegetation, litter, soil etc. Thus, even at the same geographical location, the temperature regimes experienced by fungal mycelia within different substrata and ecosystems can vary considerably, e.g. temperature within a woodland often has lower maxima and higher minima than in adjacent grasslands (Wilkins & Harris, 1946; Geiger, 1965).

Soil and litter are poor conductors of heat so the rate of penetration of heat from the surface into soil is slow. Thus, whereas the diurnal (and seasonal) temperature of the top centimetre or so of the litter closely follows fluctuations in air temperature, fluctuations decrease with depth and there is a lag in response, which can be as much as two hours per centimetre, so that at a depth of 15 cm the surface maximum at noon is reflected in a maximum at midnight (e.g. Swift, Heal & Anderson, 1979). At a depth of 30 cm fluctuations are often negligible. Similar phenomena occur in fallen branches and other bulky substrata (Fig. 4).

As the thermal characteristics of substrata result from the joint characteristics of the individual solid, gaseous and liquid components, and since water has a much higher thermal capacity than other components, the moisture content can significantly alter the temperature regime of a substratum. For instance Bocock, Bailey & Hornung (1982) found that the persistence of water in forest soils tended to reduce temperature fluctuations. They also found that temperature amplitude is higher in soils rich in organic matter than in mineral soils.

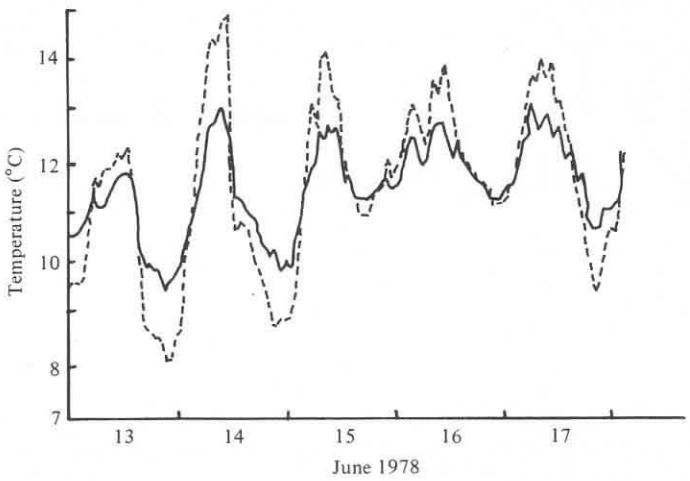


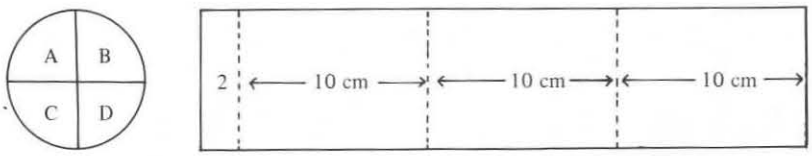
Fig. 4. Diurnal fluctuations in temperature (°C) of soil at 5 cm depth (———) and at the centre of a branch approximately 2 cm in diameter (– – – –). (From Boddy, 1983*b*.)

Trends in temperature are thus found down the soil and litter profile and within bulky substrata, but unless large differences occur in the thermal conductivities of substrata, micro-spatial variation at the same horizontal level is very slight. This, combined with the fact that it is relatively simple to obtain accurate, continuous measurement of substratum temperature, e.g. by use of thermistor probes and data recorders, enables accurate determination of the temperature regime experienced by fungal mycelia (cf. water content and gaseous composition).

Water

Micro-spatial distribution and the expression of water content. Water content is often expressed gravimetrically as a percentage of the oven dry weight of substratum; however, this cannot be used to compare the amount of water in different substrata, e.g. between a sandy and a loam soil, between different organic materials, or between wood at different stages of decay, because these do not necessarily have the same masses in equal volumes.

Because absolute water content is an easily quantifiable and easily understood term it is frequently used, but it clearly has little biological meaning so far as micro-organisms are concerned. The volume of water *per se* required for the creation of a few centimetres length of hypha will be contained in one gramme of many apparently dry soils (Griffin, 1972).



A	294	109	123
B	228	131	101
C	194	123	159
D	196	137	122

Fig. 5. Moisture profile of a small branch (<2.5 cm diameter, relative density 0.44 g cm^{-3}) from the forest floor. The dashed lines indicate the sampling positions and the figures beneath are the moisture contents (percentage oven-dry weight). Samples A and B were from the upper side and C and D from the lower side of the branch. (From Boddy, 1983*b*.)

In solid substrata water is located in the voids and the importance of water content to micro-organisms lies in the factors correlated with its presence and location. Water influences hyphal activity in two main ways: in regions of low moisture content where its lack may limit growth because of difficulties of extracellular enzymes reaching their targets and of obtaining water for other physiological activities; and, indirectly, in regions of high moisture content as a result of poor aeration.

A term which is becoming used increasingly to express the difficulty (or ease) with which water may be obtained from a substratum is that of water potential. This subject has been comprehensively treated by Griffin (1972, 1977, 1982) and will only be considered briefly here. Water potential can be regarded as having two main components: matric potential and osmotic potential. Matric potential is a result of forces associated with interfaces between water, air and the solid matrix (i.e. soil, leaf litter, wood). Osmotic potential reduces the potential energy of water by the presence of solutes within it. One of the components usually predominates to the exclusion of the other. For instance, in the sea or in syrup and preserves, the high solute content results in the osmotic component predominating. In soil and wood on the other hand, the matric component tends to predominate although dissolved nutrients will add an osmotic component and will be important in saline and heavily fertilised soils (Griffin, 1963; Williams, 1968; Boddy, 1983*c*).

In order to understand the impact of water on mycelia it is helpful to consider the distributions of mycelia and water within the substratum (e.g. those in Fig. 3). When initially saturated substrata begin to dry out water tends to be lost first from the largest voids, the smallest retaining water for the longest time (see Griffin, 1972). Concomitant with decrease in water is an increase in the gaseous phase; thus the two are intimately associated. Clearly, the void size distribution in substrata (Fig. 3) will to some extent determine the location of water and the gaseous phase and there will be considerable micro-spatial variation. Substratum matric potential will give some indication of the location of water in relation to void size and it can be measured and even maintained in experimental systems (Griffin, 1963, 1972, 1977, 1982; Rose, 1966; Holmes, Taylor & Richards, 1967; Stone & Scallen, 1967; Clarke, Jennings & Coggins, 1975). Such measurements quantify the overall moisture regime of the substratum/mycelium complex, but unless the locations of hyphae are known it reveals little at the hyphal level. Further, the distribution of water varies on a slightly larger scale

within substrata according to the wetting and drying regimes experienced by different parts. This is illustrated for a small branch lying on the woodland floor (Fig. 5) and for a short stake having one end immersed in water (Fig. 6; Baines & Levy, 1979). The latter can be considered as a model for any woody resource with parts above and below ground, e.g. a cut stump, standing dead tree.

Clearly micro-spatial and other small-scale variations are likely to be of prime importance to hyphae and mycelia; however, few data of this kind are available. Meaningful gross measures of substratum moisture content are not available; even though matric potential to some extent describes micro-spatial location of water and the force required to remove it from substrata, other small-scale variation means that at present it only serves as an alternative description of moisture content and its precise meaning may be less well understood than percentage moisture content.

Macro-spatial and temporal distribution of water in woodlands. From the above discussion it is clear that it is not a simple matter to obtain meaningful information on the distribution of water in substrata in relation to the fungal mycelium. Despite this it is possible to gain some

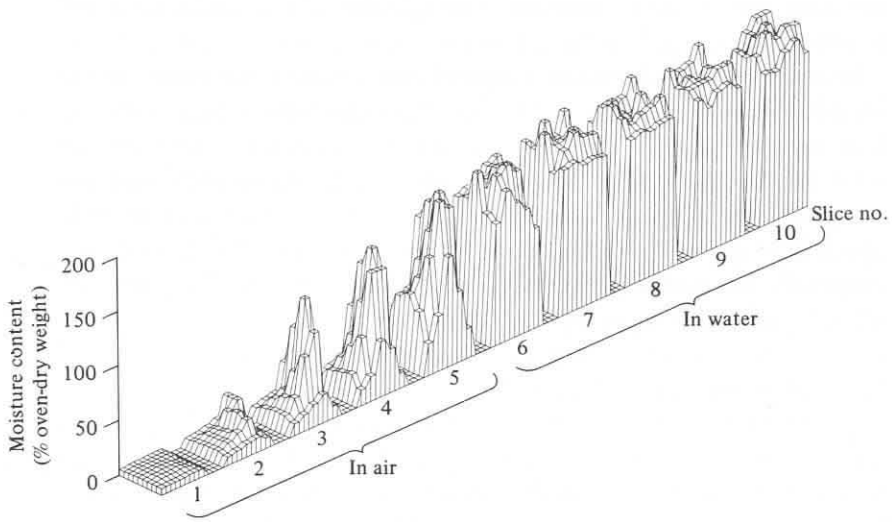


Fig. 6. Moisture profile (percentage oven-dry weight) of a short Scots pine stake (112 mm long by 20 × 20 mm square) after part had been immersed in water for 3 months at 22 °C ± 5 °C (From Baines & Levy, 1979.)

insight into the temporal and macro-spatial water regimes in woodlands from gross measurements of rainfall and percentage moisture content.

The amount and distribution of water within substrata depend upon the capacity for storage of water and its supply and loss. The capacity for storage depends on porosity which varies between substrata depending upon the anatomy, state of decay and degree of compaction. Supply of water to dead organic substrata is mainly by precipitation and loss by drainage, lateral run off and evapo-transpiration which is in turn influenced by temperature and humidity. In addition various inherent features of substrata that influence wetting and drying include: porosity; distance over which water has to travel, i.e. depth in soil, size of wood; presence or absence of bark for wood; and vegetation cover.

Temporal variation occurs as a result of local climate influencing supply and loss of water. The overall moisture relationships of the leaf litter layer have received considerable attention and accurate prediction of moisture content is now possible if precipitation and potential evapo-transpiration are known (e.g. Meentemeyer, 1974; Moore & Swank, 1975). Less information is available for other substrata but temporal variation in moisture content of small branch wood has been monitored (Fig. 7; Boddy, 1983*b*).

General statements regarding the distribution of water in woodlands can be made and large differences in water regimes would be expected to exist between substrata depending on location. For instance the quantity of water in functional sapwood (in terms of percentage water holding capacity) is always high and often considerably higher than in many dead organic substrata. Because of conditions favourable to drying, attached dead branches and leaves and standing dead trunks are generally drier than those on the forest floor, although if precipitation is light it may be intercepted in the canopy with little reaching the ground. Likewise surface litter is often drier than deeper litter, humus and other buried substrata.

Gaseous environment

The gaseous composition of substrata is the product of biological metabolic processes (thus under aerobic conditions O_2 and CO_2 are of most significance) and physical phenomena which exert their effect mainly via their influence on gaseous diffusion. The rate of diffusion within substrata is largely determined by the diffusion coefficients and the geometry of the system of voids including both the distance and shape of pathways to the external atmosphere. This will vary between

different substrata and hence gaseous regimes will differ (Boynton, 1941). Any factor which increases the effective path length will decrease the rate of gaseous exchange and in soil and litter the two most significant factors are depth and water content (Fig. 8; Boynton, 1941; Yamaguchi, Flocker & Howard, 1967; Griffin, 1963). The solubility of O_2 is 35–50 times less than that of CO_2 over the range of temperatures encountered in soils (Brock, 1966); thus waterfill of voids will have a

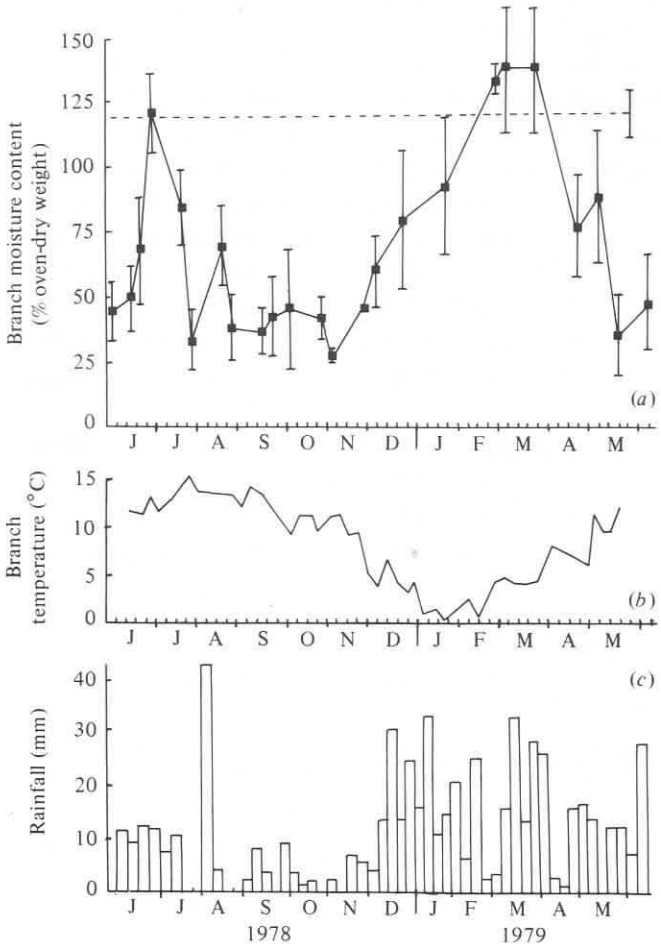


Fig. 7. Seasonal fluctuations in microclimate of small branches (1.5–2.5 cm in diameter, 15 cm long, 0.4–0.5 g cm^{-3} relative density) decaying on the floor between June 1978 and June 1979. (a) Branch moisture content (% oven dry weight ± 95% confidence limits). Hatched line indicates moisture content at saturation. (b) Branch temperature (°C). (c) Local rainfall (mm). (From Boddy, 1983*b*.)

larger effect on O_2 than CO_2. These features are illustrated for different depths in sandy loam soil columns held at different temperatures (Fig. 8; Yamaguchi *et al.*, 1967).

Similar considerations apply to other substrata such as wood, in which case path length depends on water content, anatomy, size and state of decay. In general gases penetrate undecayed wood rather slowly especially in radial and tangential directions: in *Fagus sylvatica* permeability is 65 000 times greater longitudinally than tangentially (Stamm, 1946; Smith, 1964). Permeability also differs between species, that of hardwoods usually being greater than softwoods. As decomposition proceeds the void space will increase with a concomitant decrease in path length.

As a result of these features differences in the overall gaseous composition exist between substrata: in humus and litter relatively little CO_2 accumulates under normal conditions (Romell, 1928, cited in

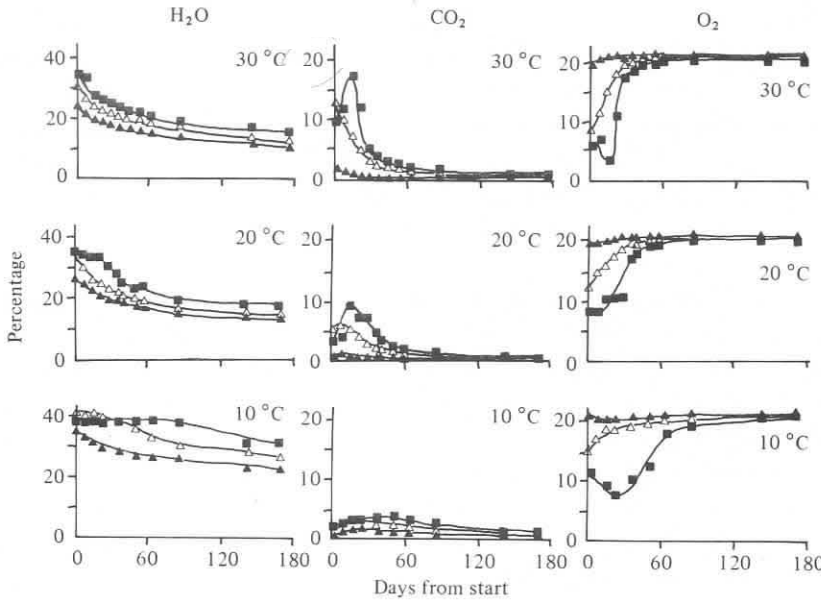


Fig. 8. Relationship between temperature, moisture content (% volume), CO_2 concentration and O_2 concentration, with time following initial saturation of sandy loam soil columns at depths of 5 cm (▲), 35 cm (△) and 65 cm (■) from the surface. (From Yamaguchi, Flocker & Howard, 1967, *Soil Science of America, Proceedings*, volume 31, 1967, pages 164–7, by permission of the Soil Science Society of America.)

Hintikka, 1982; Brierley, 1955) whereas in living or dead wood concentrations are often much higher than in air, commonly being in the region of 10–20% (Chase, 1934; Thacker & Good, 1952; Jensen, 1967, 1969*a*; Hintikka, 1982; Hintikka & Korhonen, 1970). Carrodus & Triffet (1975), using more sophisticated techniques, found that the gas in living *Acacia* stems was almost pure CO_2. In most examples increase in CO_2 is accompanied by a concomitant decrease in O_2. Seasonal fluctuations in gaseous composition often occur (Chase, 1934; Boynton, 1941; Paim & Beckel, 1963; Jensen, 1969*a*) resulting from seasonal changes in temperature, moisture and respiratory activity.

The above is based on bulk sample data of the gaseous phase. Mycelia are however, often bathed in water and in these conditions it is the quantity of dissolved gases that is significant but, as is so often the case, micro-spatial data are lacking so that conditions at the hyphal and mycelial level are unclear. That considerable micro-spatial variation is likely to exist is apparent from the discussion on water and a striking example is given by Greenwood & Goodman (1967) who showed that even in the best-aerated soils, anaerobic conditions exist in water-saturated soil crumbs if their radii are greater than 3 mm. Gaseous composition on a micro-scale *in situ* could now be investigated using such techniques as mass spectrometry using probes with Teflon membranes (Lloyd, Scott & Williams, 1983) and by using micro-electrodes (e.g. Wimpenny & Coombs, 1983).

pH

Hydrogen ion concentration in substrata is affected by several factors including water regime, salt concentration, CO_2 concentration, and number of exchangeable cations present. Its influence on gaseous environment is described below, but it is one of the most difficult environmental factors to enumerate and understand. The pH of substrata is usually given as a single value, or range of values, but it varies considerably between microhabitats and such measurements are relatively meaningless. No further consideration will be given to pH here but a good account is presented by Swift *et al.* (1979).

Interactions between abiotic variation

As has already been indicated the abiotic variables are intimately associated; thus change in one will often influence another. The following examples serve to emphasise this. Temperature affects drying of substrata, which by shortening diffusion-path length indirectly affects

gaseous composition. Gaseous composition is further affected by temperature as the solubilities of both O_2 and CO_2 increase with decrease in temperature. Gaseous composition is also affected by the tendency of CO_2, but not O_2, to dissociate in water into a number of ionic forms, the relative frequency of which is markedly influenced by temperature and particularly by pH

$$CO_2 \text{ (gaseous)} \rightleftharpoons CO_2 \text{ (dissolved)} + H_2O \rightleftharpoons H_2CO_3 \rightleftharpoons H^+ + HCO_3^- \rightleftharpoons CO_3^{2-} + 2H^+$$

At or below pH 5 only dissolved CO_2 is significant but the equilibrium moves to the right with increasing pH; the ~~bicarbonate~~ carbonate ion is the predominant form between pH 7 and pH 10 (Brock, 1966). Thus for hyphae, which are usually bathed in a water film, measurement of gaseous CO_2 in the substratum atmosphere is not sufficient for elucidation of the conditions actually experienced. Simultaneous measurements of pH and CO_2 would remedy this but such joint measurements are rarely made. This may not be too problematic in litter as many are acidic (Williams & Gray, 1974; Swift *et al.*, 1979).

Effect of decomposer organisms on abiotic variables

That abiotic variables affect decomposer organisms is obvious, and will be discussed in detail later, but the converse is sometimes forgotten. In general, temperature is not significantly affected by the activities of micro-organisms as their output of metabolic heat is low and is usually dissipated fairly rapidly. Instances when this is not so usually arise in association with man's activities particularly in very compact substrata, a striking example being in compost heaps where temperatures greater than 60 °C may develop as a result of microbial activity.

Moisture content and gaseous composition on the other hand can be, and presumably often are, altered considerably. Water is, for instance, liberated during the breakdown of cellulose. Griffin (1977) states that complete microbial decomposition of 1.0 g yields 0.555 g water. Mycelia can translocate water to and from substrata, a prime example being that of the dry rot fungus *Serpula lacrimans* (Jennings, 1982; and Chapter 7).

Effect of microclimate on the activity of basidiomycete mycelia in culture and natural substrata

Several authors have described the influence of abiotic variables on gross decomposition rates (e.g. Bunnel, Tait, Flanagan & Van Cleve, 1977; Boddy, 1983*c*). At best these measurements give only an

estimate of 'average' microbial activity in substrata within which may exist a variety of nutritional and climatic micro-environments supporting activity at widely differing levels. Few data are available for mycelial activity in the field but a preliminary picture can be built from laboratory-based studies and the few available field studies.

Temperature

Temperature influences mycelia by its effect on enzyme-catalysed reactions, and is often quantified in terms of linear extension on agar at constant temperatures. This has been reviewed by Wagener & Davidson (1954) and Cartwright & Findlay (1958) for wood-rotting basidiomycetes but not to my knowledge for litter-rotting species. Responses can be quite variable but many are mesothermic having cardinal temperatures in the region of 5°, 25° and 35 °C (Fig. 9). Linear extension rates at optimum temperature can also vary considerably between species with wood-rotting fungi often extending faster than leaf-litter decomposers (Hintikka & Korhonen, 1970). Contrary to popular belief, extension may often be quite fast, e.g. optimum extension of *Bjerkandera adusta* is 12 mm day^{-1} and *Stereum hirsutum* is almost 9 mm day^{-1} (Boddy, 1983*a*). It would be wrong to give the impression that little extension occurs at low temperatures in woodlands: *Clitocybe flaccida* and several other litter-rotting species have optima at or below 20 °C and maxima at about 25 °C (Fig. 9; Hintikka, 1964). Mitchell (unpublished) found considerable extension of fairy ring mycelia and Thompson (Chapter 9) of cord systems during winter months in Britain. Hintikka (1964) found a number of psychrophilic or psychrotolerant Basidiomycotina growing and decomposing leaf litter beneath the snow cover throughout the winter in Finnish woodlands. He observed that several of these species produced aerial mycelium, which formed dense tufts and rhizomorph-like structures when growing on agar at 5° and 10 °C but not at room temperature, and suggested that this response would aid the fungus in colonising freshly fallen litter in autumn.

Liese (1931) (cited in Cartwright & Findlay, 1958) exposed 90 different isolates of wood-rotting Basidiomycotina to temperatures of −32 °C for 14 days and found that, with the exception of some isolates of *Serpula lacrimans* (an unusual fungus in nature), all renewed vigorous growth after exposure. It seems unlikely, therefore, that mycelia of these and probably also of litter-decomposers, would be killed by low temperatures in temperate woodlands. Likewise lethal high tempera-

tures are unlikely to occur apart from occasionally in exposed situations such as branches, where there are gaps in canopy or in felled areas.

Caution must be applied, however, when extrapolating from agar to natural substrata. Temperatures optimal for linear extension on agar may not be the same for biomass production, ability to decompose cellulose and lignin, etc. For example, it has been noted that the most rapid decay of wood often occurs 2–3 °C below the optimum for extension on agar (Gauman, 1939, cited in Cartwright & Findlay, 1958; Henningson, 1968). Further, laboratory experiments are usually performed at constant temperatures whereas fluctuations are the rule in natural substrata: Jensen (1969*b*) found an increase in growth of two wood-rotting Basidiomycotina under a fluctuating regime which was not completely accounted for by the additive effect of temperature.

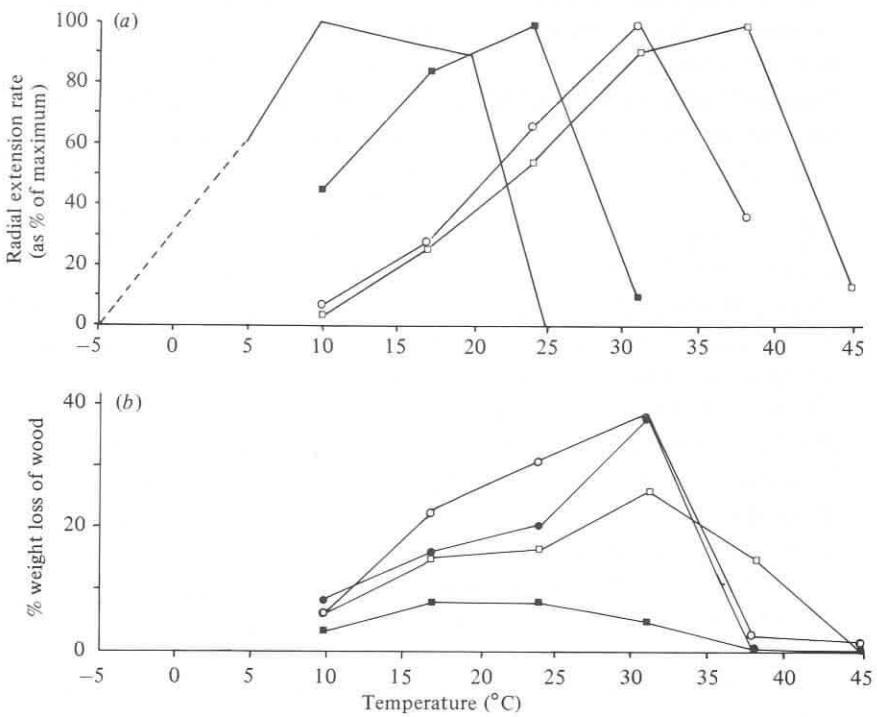


Fig. 9. Range in temperature response of selected basidiomycetes. (a) radial extension rate as a percentage of maximum, (b) decay rate of lodgepole pine wood: by a psychrophilic isolate (no symbol, From Hintikka, 1964), *Coniophora puteana* (●), *Lenzites saepiaria* (○), *Phlebia phlebioides* (□), and *Stereum sanguinolentum* (■). (From Loman, 1962, *Canadian Journal of Botany*, volume 40, pp. 1545–59, by permission of the National Research Council of Canada.)

Low water

The effect of low water on mycelia is often assessed by altering the water potential of the growth medium. Theoretically the effect of water potential on mycelia will not differ whether it is altered by osmotic or matric means (Griffin, 1972); thus either may be used. In practice, however, fungi are usually less affected by reduced osmotic, compared to matric, potentials probably as a result of solute or enzyme-diffusion problems (Griffin, 1972). When growth of mycelia is measured on agar media, the osmotic potential of which has been altered, it is essential to ensure that the effect of adding a solute is purely osmotic. Thus, several different solutes are used for comparison. Recent studies indicate that the lower limit for growth of wood- and litter-decomposing basidiomycetes is in the region of −4.0 MPa (Fig. 10; Dubé, Dodman & Flentje, 1971; Tresner & Hayes, 1971; Griffin, 1977; Wilson & Griffin, 1979; Boddy, 1983*a*, unpublished). The use of glycerol as solute allowed growth at much lower potentials probably due to the fact that polyols in general act as osmoregulators inside the cytoplasm and have the ability to preserve enzyme function (Brown, 1978).

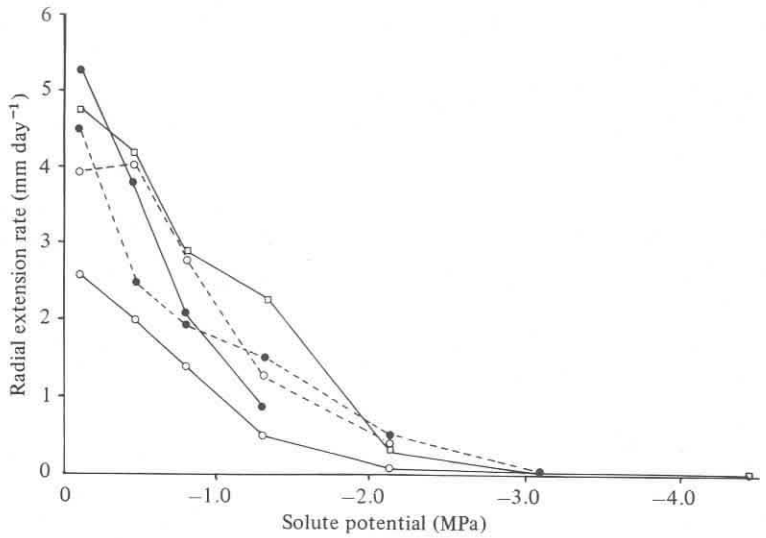


Fig. 10. Relationship between water potential (produced by KCl in malt agar) and radial extension rate (at 25 °C) of five basidiomycetes: *Exidia glandulosa* (●——●), *Hyphoderma setigerum* (●– – –●), *Phanerochaete velutina* (□——□), *Schizopora paradoxa* (○——○), and *Vuilleminia comedens* (○– – –○). (From Boddy, 1983*a*.)

By contrast with these data Wilson & Griffin (1979) found that six basidiomycetes probably from Australia (*Suillus luteus, Lycoperdon* sp., *Lactarius deliciosus, Clitocybe eucalyptorum, Geastrum* sp. and *Agaricus langei*) could withstand solute potentials below −10 MPa. Bavendamm & Reichelt (1938) found that most species that they tested grew at −14.5 MPa but these data require corroboration as the method of water-potential control was probably unsatisfactory (Griffin, 1977). Many non-basidiomycete 'soil fungi' can grow in the range −4 to −10 MPa (Griffin, 1972) and some are even able to grow below this, e.g. *Fusarium moniliforme* (Sommers, Harris, Dalton & Gardener, 1970), *Aspergillus* sp. (Pitt & Hocking, 1977).

Few data are available using other measures of activity but Griffin (unpublished, cited in Griffin, 1977) found that dry weight increase closely paralleled radial extension at various water potentials for *Gloeophyllum trabeum (= Lenzites trabea)* and *Fomes lividus*. Direct data for cellulolysis and decay rate are lacking but Griffin (1977) suggests, on the basis of work done with marine fungi (Byrne & Eaton, 1972; Meyers & Reynolds, 1959), that cellulolysis *per se* is likely to be unaffected by decrease in water potential in the range 0 to −2.8 MPa and probably even somewhat lower. Thus both growth and cellulolysis probably occur in the range 0 to −4 MPa if the physical form of the substratum in terms of void-size distribution is suitable. A critical size is that which is too small to allow diffusion of enzymes or products of degradation when holding water. Griffin (1977) suggested that in wood the limiting value for substrate availability, hyphal growth and cellulolysis might be taken as about −4 MPa. Thus, it is interesting, in evolutionary terms, that the lower limit for growth of wood-decay fungi is at about the same matric potential at which the structure of wood makes cellulose inaccessible to enzyme molecules.

Gaseous environment

Numerous studies have been performed on the effect of CO_2 on growth of basidiomycete mycelia. One of the earliest was that of Bavendamm (1928) who states that 19% CO_2 inhibits the growth of both parasitic and saprotrophic wood-rotting species but does not kill them, and also that white-rot fungi were relatively insensitive to high levels of CO_2 whereas brown-rot species were sensitive (Bavendamm, 1928, cited in Schanel, 1976). Recent studies have indicated that wood-decay species are considerably more tolerant of increase in CO_2 than litter decomposers (Hintikka & Korhonen, 1970; Schanel, 1976; Rawles,

Boddy & Rayner, unpublished). For non-wood-rotting species the maximum tolerable concentration of CO_2 was around 20–30% whereas many wood-rotting species grew well at 70% CO_2, and several that are frequently found in living or recently dead wood, were still able to grow, albeit very slowly, at approaching 100% CO_2. At concentrations around 10% the growth of many wood-rotting species was markedly stimulated as was the production of laccase and peroxidases in *Pleurotus* (Schanel, 1976). Similar effects have also been shown on the rate of mycelial biomass production (Zycha, 1937; Hintikka & Korhonen, 1970).

Hyphal and colony characteristics often alter at CO_2 concentration much above atmospheric (Hintikka & Korhonen, 1970; Schanel, 1976). Dovrtěl (1975) found changes in hyphal diameter, shape and frequency of clamp-connections at 30% CO_2, and Rawles, Boddy & Rayner (unpublished) observed the production of numerous small 'bud-like' branches on the hyphae of *Phlebia radiata, Phlebia rufa* and *Stereum gausapatum* at CO_2 concentrations above 60%.

There is some evidence that Basidiomycotina are relatively tolerant of low O_2, many being able to grow at below 1% O_2 (Bavendamm, 1928; Scheffer & Livingstone, 1937; Jensen, 1967). In the complete absence of O_2, *Serpula lacrimans* died in 2–3 days whilst 'pathogenic' fungi survived longer; *Stereum frustulatum* was the most resistant, remaining undamaged after 10 days (Bavendamm, 1928). *Heterobasidion annosum* grew well in trace amounts of O_2 (Gunderson, 1961) as did *Phlebia radiata* and *P. rufa* although 14 others failed to grow (Rawles, Boddy & Rayner, unpublished). Under such conditions anaerobic respiration may occur with the build-up of products such as ethanol, methanol, formate, acetate, lactate, and propionate. Hintikka (1969) found that wood-rotting basidiomycetes grew at slightly higher alcohol concentrations than did litter-decomposers, and there was a distinct difference in their tolerance of acetate: growth of soil- and litter-inhabiting species ceased at 0.025–0.05% whereas wood-rotters could tolerate 0.1–0.2%. Similar differences were found with formate and propionate.

Rypacek (1966) investigated aeration requirements in natural substrata by growing fungi in strips of wood having a moisture gradient. He was effectively looking at a gradient of air-filled void spaces and he estimated, by noting the wettest segment in which growth occurred, that the limit for wood-rotting Basidiomycotina was in the region of 10–20% air.

Interactive effect of abiotic variables on basidiomycete mycelia

In the field abiotic variables do not act independently upon fungal mycelia but jointly. However, relatively few studies have considered the effect of more than one variable at a time. Strong interactions between abiotic variables have been demonstrated for some fungi: for instance, in general the optimum temperature for radial growth increases by about 5 °C as water potential decreases (Ayerst, 1968; Griffin, 1978); a synergistic effect of combined lowering of O_2 and raising of CO_2 concentration has been reported in some fungi (Tabak & Cooke, 1968).

Distribution of basidiomycete mycelia in nature

The pattern of distribution of basidiomycete mycelia in woodland varies both spatially and temporally. In studies of fungal colonisation of individual resource units Basidiomycotina have often been reported as occurring relatively late in the so-called 'succession' (e.g. see Frankland: Chapter 11; Rayner & Webber: Chapter 18). These ideas have emerged largely as a result of the method of study and have, to a large extent, obscured the role of basidiomycete mycelia in the decomposition of plant and animal remains. This topic is discussed more fully by Cooke & Rayner (1984), suffice it to say here that their temporal distribution, i.e. community development, requires much further study and careful re-evaluation of ideas. Temporal patterns will be mentioned here only briefly in relation to microclimate.

The heterogeneous distribution of different substrata within woodlands and their associated microclimates results in considerable spatial variation in the distribution of basidiomycete mycelia. The distribution of these is now beginning to receive some attention particularly in bulky woody resource units (e.g. Rayner & Todd, 1979; Boddy & Rayner, 1983*a*,*b*; Coates, 1984) although less information is available for litter (Frankland: Chapter 11; Thompson: Chapter 9). However, there is clear indication that microclimate does to some extent influence the distribution of basidiomycete mycelia.

In temperate woodlands distribution is not usually likely to be much affected by high temperatures as these rarely rise much above those optimal for activity, although this may not be the case in exposed conditions. For instance, in a study of the distribution of decay fungi within logging slash in Canada, Loman (1962, 1965) found that the four most common basidiomycetes were remarkably consistent in their spatial location. Thus, *Lenzites saepiaria* was predominant in the central

portions of the slash; *Phlebia phlebioides* was isolated mainly from upper portions; and *Stereum sanguinolentum* and *Coniophora puteana* from the lower portions. This distribution may be explained, at least in part, on the basis of their temperature tolerances, optima for growth, and relative decaying abilities (see Fig. 9). High temperatures lethal to the mycelium of *C. puteana* and *S. sanguinolentum* but not to *L. saepiaria* and *P. phlebioides* occur in the upper and central portions of slash during fine weather. Also, *P. phlebioides* had a much higher growth rate and decay rate, at 38 °C, than the other three species, and *L. saepiaria* caused more decay than the others at 31 °C. At 10 °C the greatest decay was caused by *C. puteana*. A further possibility is that the outcome of combative interactions between these fungi may vary according to temperature (cf. Rayner & Webber: Chapter 18).

Water appears to be a major determinant of both activity and distribution, either directly in the low water content region or indirectly in the high region. Low moisture content is likely to be particularly important in standing dead plant tissues and in the surface layer of fallen litter. As many Basidiomycotina do not appear to be able to grow at low water potentials those which predominate in such habitats may do so largely as a result of their ability to survive such conditions, mycelial activity only occurring under improved conditions. It is likely that this is the case for *Hyphoderma setigerum* and *Schizopora paradoxa*, two species which are usually found associated with conditions prone to desiccation in attached oak branches and trunks (Boddy, 1983*a*; Boddy & Rayner, 1983*a*; Boddy & Thompson, 1983). Many of the most active litter-degrading fungi which are not component restricted, e.g. *Collybia* spp., *Clitocybe* spp., and many cord-forming fungi, grow beneath the current year's litter where substrata are more compacted and moisture conditions are presumably more stable. Here the mycelium grows as luxuriant wefts, sheets and cords which often show maximal development during winter, extension appearing to be more dependent on moisture than temperature (Karenlampi, 1971; Thompson & Rayner, 1982, 1983; Mitchell, unpublished).

At the other extreme it is well known that waterlogging limits decay (e.g. Cartwright & Findlay, 1958; Boddy, 1983*c*). However, in temperate woodlands, although moisture contents high enough to limit decay do occur periodically (e.g. Fig. 7; Boddy, 1983*b*), it is unlikely that this would affect the distribution of mycelia, provided that it was not a permanent feature. In living tissues, on the other hand, the substratum is usually permanently saturated and Boddy & Rayner (1983*c*) have

advocated that this explains the confinement of decay to non-functional sapwood in living trees.

The different tolerances of Basidiomycotina to elevated levels of CO_2 also reflect their occurrence in nature: soil- and litter-inhabiting species are generally much less tolerant than wood-rotting species (Hintikka & Korhonen, 1970), correlating with conditions found in such environments. Gaseous composition may explain why species such as *Marasmius androsaceus* and *Mycena galopus* grow on leaf litter and twigs but not on tree trunks. Even more tolerant of high CO_2 were species commonly found in attached branches (Boddy & Rayner, 1983*a*; Rawles, Boddy & Rayner, unpublished), which is probably related to their ability to colonise partially living or recently dead tissue. These basidiomycetes form extensive individuals in an apparently very short time which cannot be accounted for in terms of mycelial extension (Boddy & Rayner, 1982, 1983*a,b,c*) and it has thus been suggested that the fungi become distributed through the sapstream by modules which are only capable of very limited growth until the branch is stressed (Boddy & Rayner, 1983*c*; Cooke & Rayner, 1984). The small buds produced on hyphae of these fungi under high CO_2 concentrations may possibly serve such a purpose.

Armillaria spp. tend to become established in cut stumps and suppressed trees before cord-forming fungi (Rayner, 1975; Thompson & Boddy, 1983; Thompson: Chapter 9), a phenomenon which has been explained on the basis that *Armillaria mellea* is pathogenic and that other *Armillaria* spp. act as weak pathogens, whilst cord-forming fungi act purely saprotrophically. This ability may however be explained in terms of gaseous (in particular O_2) relations; Smith & Griffin (1971), in a comprehensive study of *Armillaria elegans,* demonstrated the importance of gaseous composition and water in growth and development of rhizomorphs. *Armillaria* rhizomorphs consist of a complex meristematic apex behind which is formed a hollow tube, surrounded by walls of closely-packed hyphal cells. They demonstrated that for optimal growth the rhizomorph required a high partial pressure of O_2 within the apex but a low one outside (otherwise melanisation took place and prevented growth). These apparently contradictory conditions are achieved by growth through moist soil and litter with the hollow rhizomorph allowing O_2 to diffuse to the tip by remaining in contact with wooden substrata in gaseous continuity with the atmosphere. Further, when crossing gas-filled voids, rhizomorphs produce short side branches which allow access of O_2. Field data did not suggest any marked

reduction in growth in near-saturated soils (Griffin, 1972). Thus it might be expected that *Armillaria* spp. would be able to gain access to woody tissues before other fungi that do not have a route for direct access of O_2.

Microclimatic variables do not, by a long way, explain the distribution, and activity, of all Basidiomycotina. In nature many species are specific to certain kinds of litter whereas in pure culture they do not show strong preferences (Hering, 1982). Such restriction to a particular niche may be due to interaction with other organisms (Frankland: Chapter 11; Rayner & Webber: Chapter 18), and considerable further study is required for complete elucidation.

Conclusions

This brief account has indicated that organic substrata in woodlands consist of a mosaic of microsites, differing in terms of microclimatic parameters of temperature, moisture content, gaseous composition and pH. Field data for microclimate at this level are lacking, and information on activity of mycelia under various microclimatic regimes is largely confined to studies on relatively homogeneous artificial media in the laboratory. Further, the actual distribution of basidiomycete mycelia in nature has been little studied. Despite this, some indication of activity and distribution of mycelia in relation to microclimate has been possible. However, it is clear that the time is ripe for these gaps in our knowledge to be filled.

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